

# Developmental Trends in the Post-Embryonic Development of Lithobiomorph Centipedes

*Alessandro MINELLI, Enrico NEGRISOLO & Giuseppe FUSCO*

Dipartimento di Biologia, Università di Padova, I-35121 Padova, Italy

## ABSTRACT

The problem of comparing individual developmental stages of related species undergoing a different number of moults is tentatively settled by taking as developmental time units both major developmental periods, the first being between hatching and the transition from the last larval to the first postlarval stage, and the second between the first postlarval stage and the first mature stage. On such a re-scaled developmental schedule, the developmental trajectories of several characters in different species are studied, based on ANDERSSON's (1979) data. This analysis revealed extensive heterochrony, as did further comparisons of metric and meristic characters in mature specimens belonging to 62 species, with adult length ranging from 6 to 35 mm.

## RÉSUMÉ

### Modalités du développement post-embryonnaire des chilopodes lithobiomorphes.

Afin de résoudre le problème de la comparaison entre les stades de développement d'espèces présentant un nombre différent de mues, les auteurs utilisent en tant qu'unités temporelles les deux étapes fondamentales du développement : d'une part la phase allant de l'éclosion jusqu'au passage des stades larvaires aux stades post-larvaires, d'autre part la phase allant du premier stade post-larvaire jusqu'à la maturité sexuelle. La comparaison des trajectoires ontogénétiques de plusieurs caractères chez différentes espèces (données d'après ANDERSSON, 1979) révèle plusieurs cas d'hétérochronie. D'autres hétérochronies sont mises en évidence par la comparaison de plusieurs caractères métriques et méristiques entre des exemplaires adultes appartenant à 62 espèces, pour lesquels la longueur varie de 6 à 35 mm.

## INTRODUCTION

The overall uniformity of body structure within all recent Lithobiomorpha, and especially within *Lithobius* s.l., where a great many species just seem to be "minor variations on a common theme", provides the scope for investigations of structural and morphogenetic constraints in the evolution of form. However, current knowledge of post-embryonic development of lithobiomorph centipedes is still in its descriptive phase; cf. especially the detailed studies of ANDERSSON (1979, and literature cited therein). Many additional, even basic aspects still need investigation, but we think that many insights, at least of a qualitative nature, can be obtained from a careful consideration of the extant evidence.

## MATERIALS AND METHODS

We have mostly relied on literature data, but for the measures of individual podomeres in legs 1-15, we have studied *L. microps* Meinert (a female from Italy: Miogliola (AL)) and *L. forficatus* (Linnaeus) (a male from Italy: Bosco della Mesola (FE)). Two (a, b) main data bases have been collected: (a) head length (HL), body length (BL), number of ocelli (OC), number of antennomeres (AN), number of coxal pores (CP), number of coxosternal teeth (CT), number of setae on the first genital sternite of the male (SGM), id. of the female (SGF), in each post-embryonic stage of *Lithobius forficatus* (Linnaeus, 1758), *L. erythrocephalus* C. L. Koch, 1847, *L. melanops* Newport, 1845, *L. crassipes* L. Koch, 1862, *L. microps* Meinert, 1868, *L. calcaratus* C. L. Koch, 1844, *L. curtipes* C. L. Koch, 1847 and *L. tenebrosus* Meinert, 1872 (data compiled from ANDERSSON, 1979); (b) BL, OC, AN, CP, CT, total number of spines on the legs of one side of the animal (ST) and plectrotaxy (distribution of the individual spines on all pairs of legs) in the adults of the 62 species listed in the Appendix (data compiled from BROLEMAN, 1930; EASON, 1964; MATIC, 1966; ANDERSSON, 1979).

As for the methods, the less trivial points are the re-scaling of ontogenetic stages onto a normalized x-axis, as justified in the next section and explained also in the legend to Figure 1, and the standardization of the values of BL, OC, AN, CP, CT and ST before using them in multivariate analysis (principal components).

## RESULTS

*Comparability of ontogenetic stadia*

When comparing the ontogenetic stadia of different, although closely related, arthropod species, the first question to answer is which stage of species B, if any, is more correctly and meaningfully comparable with a given stage of species A. Simply referring to the ordinal number of the stage (i.e., to the number of moults the animal has undergone) does not seem to be safe, because of the different number of stages that A and B may possibly go through before getting maturity, or during their whole life. We could even be faced with intraspecific variation in the number of post-embryonic stages. One of us (MINELLI, 1992) had already looked for a possible application to centipedes of GRANDJEAN's (1951) concept of *stase*, but could not find a fixed set of structurally distinct stages, independent from the number of moults occurring between any two of them.

We believe that only three points, along the post-embryonic development of all lithobiomorphs, can be more or less safely compared across species. These are the first larval stage (L0 in ANDERSSON's terminology), the first post-larval stage, i.e. the first stage with the full complement of segments and legs (PL1)  $\Delta$ , and the first mature stage. The identification of the onset of maturity is not easy to assess in objective terms. For the species whose developmental schedules we have compared, we have simply accepted, for operational reasons, the estimates of maturity as given by ANDERSSON (1979), although his assessments were derived (but for *L. forficatus*) from comparative guesses rather than from objective, e.g. histological, proofs.

On this basis, we have re-scaled the post-embryonic stages of all species onto a common scale. We have dealt separately with the two intervals, the first between L0 and PL1, the second between PL1 and the first (guessed) mature stage (Fig. 1). For the species under study, this causes no relative changes between hatching and PL1, because the number of larval stages is always the same, whereas the individual post-embryonic stages of the different species account for different percentages of the normalized development. Some characters, e.g. head length, follow similar ontogenetic trajectories in all species, but others are subjected to heterochrony, at least for some species. Ontogenetic trajectories for ocelli start at different points, but subsequently evolve in comparable ways. In still other cases, as for the setae of first genital sternite in both sexes, heterochrony is given by the different speed of comparable ontogenetic changes that start at the same time. Again, as for the number of antennomeres, the first steps are the same in all species under comparison, but their further increase goes on at different speed; however, the different trajectories of antennomeres in *L. calcaratus* (or in *L. forficatus*) and *L. tenebrosus* coincide again at the end. The passage from larval to post-larval stages seems to be a major change only for those characters whose phenotypic expression requires the presence of

fully developed segments XII and following (e.g., the number of setae on first genital sternite); and that, not for all species.

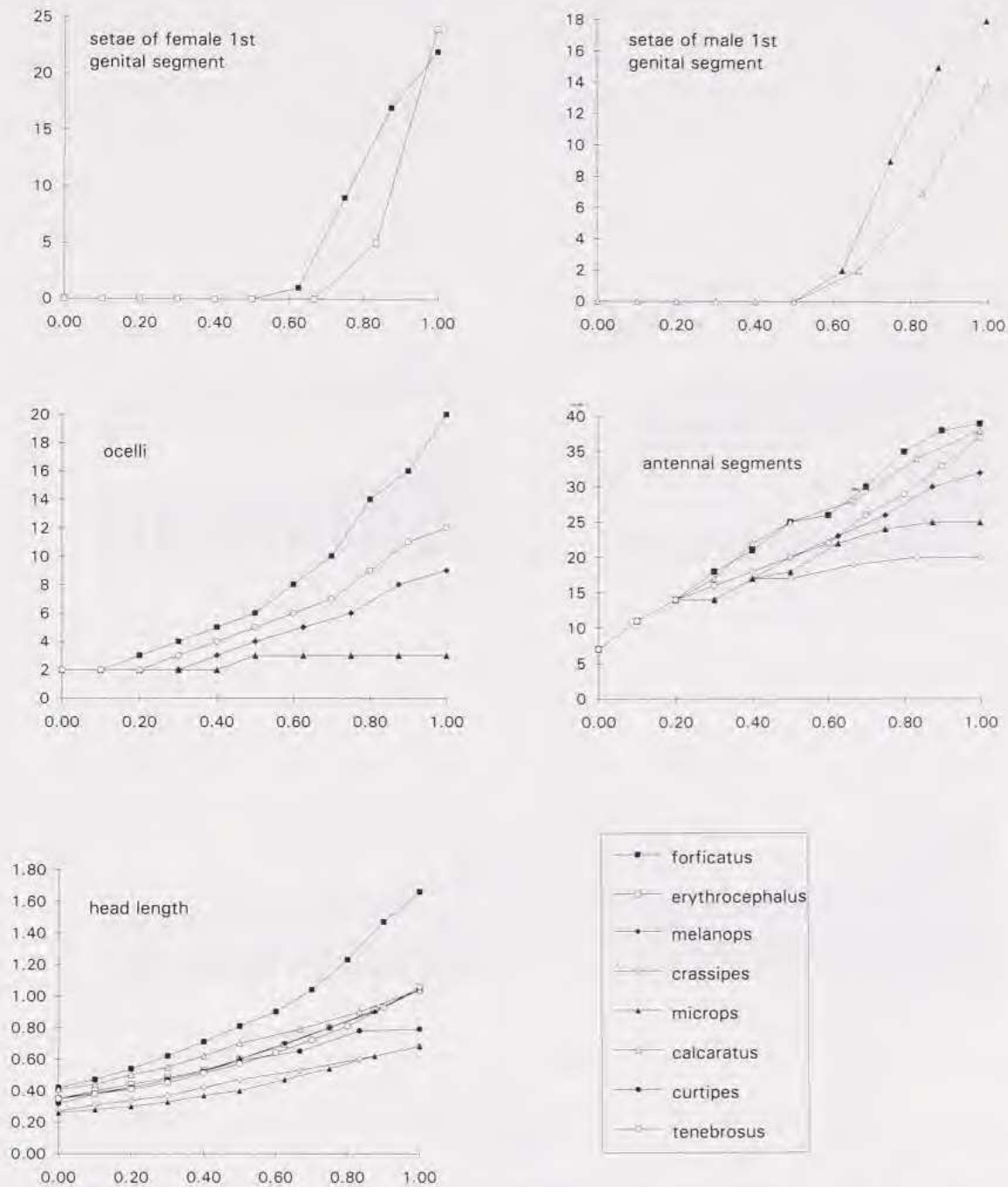


FIG. 1. — Ontogenetic trajectories for individual characters in selected *Lithobius* species. Data after ANDERSSON (1979). Horizontal axis represents normalized post-embryonic development, with first larval stage (L0) and first mature stage (guessed), respectively, at the two ends of the scale; mid-point of the x axis corresponds to PL1. Individual points along the trajectories refer to the individual post-embryonic stages, whose number before maturity is different in the different species. Head length in mm.

*Comparisons of mature representatives of species of different size*

Further comparisons have involved a comparable (mature) stage of 62 species (see Appendix) ranging in length from 6 to 35 mm. We have tried to identify the occurrence of coherent trends of variation of different structural traits, as well as the independence of other traits.

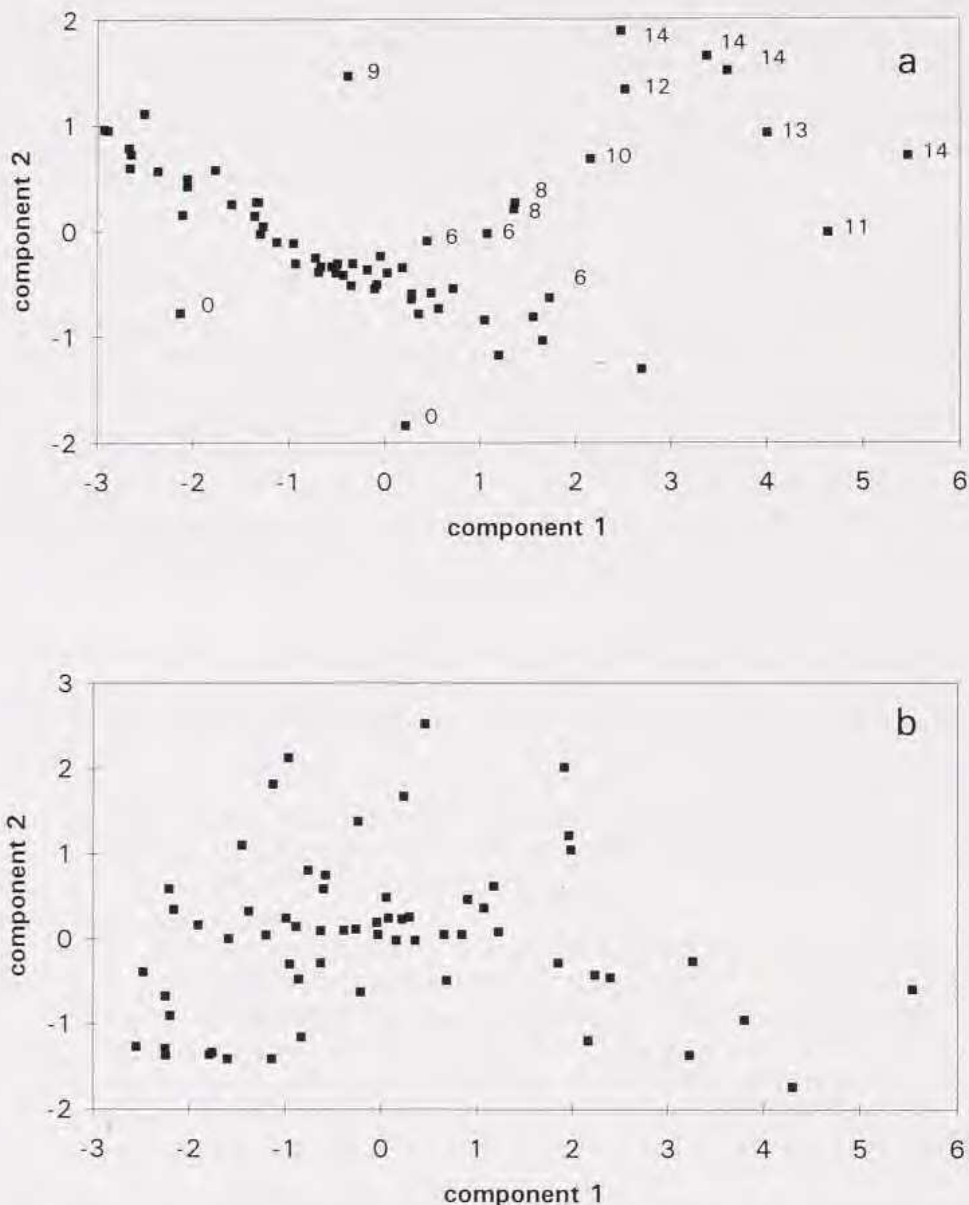


FIG. 2. — Scatter plot of the 62 *Lithobius* species listed in the Appendix onto the plane of principal components 1 and 2, the original variables being in (a) BL, OC, CP, CT and ST, in (b) BL, OC, CP, CT and AN. In (a), the percentual contributions of the first two principal components to total variance are, respectively, 72.6 and 11.5; in (b), the corresponding values are 64.0 and 18.0. In (a), the numbers within the plot identify the average number of CT; squares without numbers are for the species with CT=4.

If we place the 62 species in the morphospace identified by the following 5 variables: BL, OC, CP, CT, ST in a plot of principal components 1 and 2 (Fig. 2a), we see a very coherent distribution, with points seemingly arranged in parallel rows, each of them corresponding to an "isodont line", along which are aligned the species with the same number of coxosternal teeth.

The number of antennomeres does not behave as these five characters. Figure 2b shows the disruptive effect of substituting AN for ST in the set of original variables. That means, that the antennae are not subjected to the same constraints as the other four variables.

Thus, these interspecific comparisons provide further evidence for heterochrony, because of the different variation of individual characters with size at maturity.

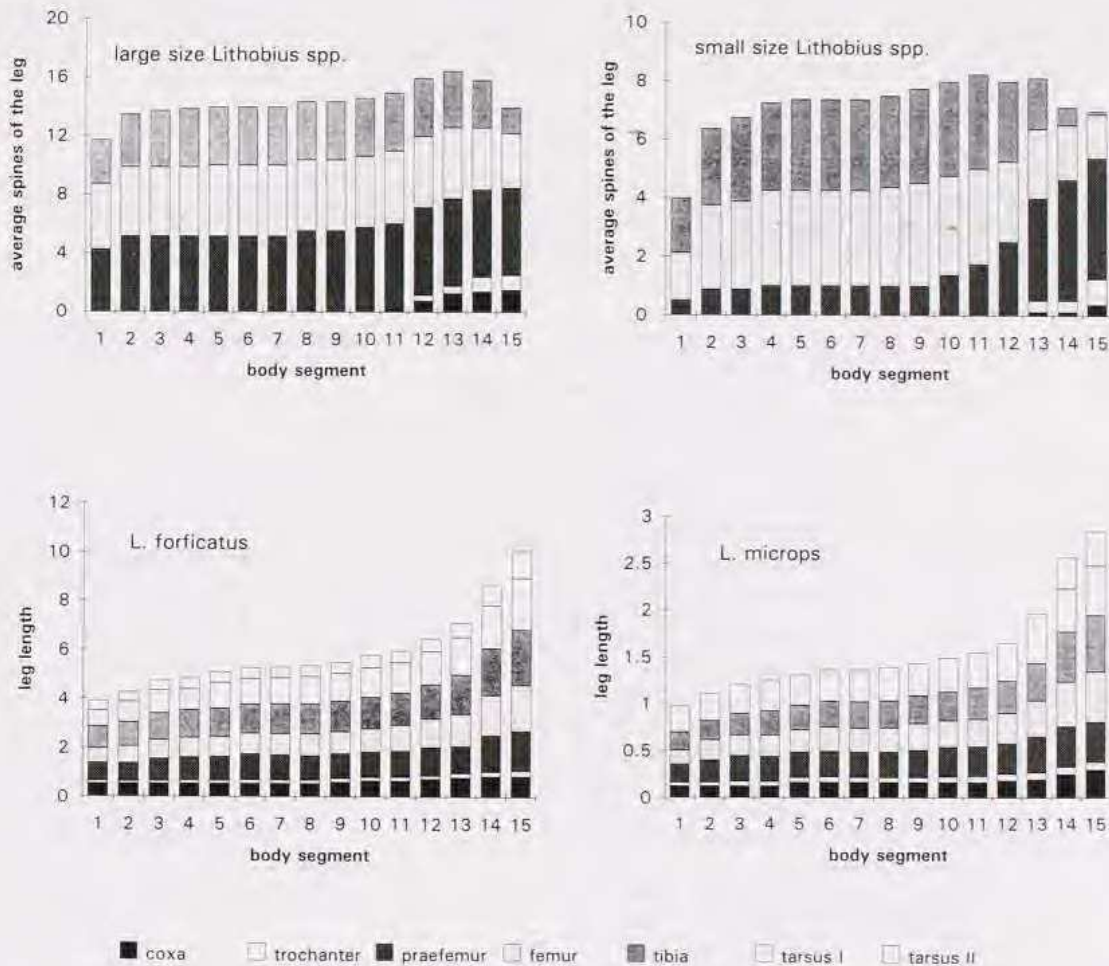


FIG. 3. — Plectrotaxy and leg length. Bar diagrams in the upper row give the mean number of spines per podomere (coxa to tibia) per leg (I to XV) in the eight largest species listed in the Appendix (left) and in the seven smallest species of the same list (right). Bar diagrams in the under row give the length (mm) of the individual podomeres in each leg (I to XV) in one individual of a large species (left: *Lithobius forficatus*, male) and in one individual of a small species (right: *Lithobius microps*, female).

Size at maturity has also an effect over the segmental pattern of distribution of leg spines. In the small species (Fig. 3, upper row, right), the average number of spines per leg increases steeply from segment I to segment III, goes on with trifling differences until segment IX or X, peaks at XI, then slowly decreases, whereas in the large species (Fig. 3, upper row, left) a "near-saturation" is soon reached on leg II. The prefemur is most responsible for the changes in the number of spines throughout the segments.

Changes in spinulation of the proximal podomeres (coxa and trochanter) of all species and especially of the prefemur of small species parallel leg length changes along the body. However, leg length profiles are not different in small vs. large species (Fig. 3, under row).

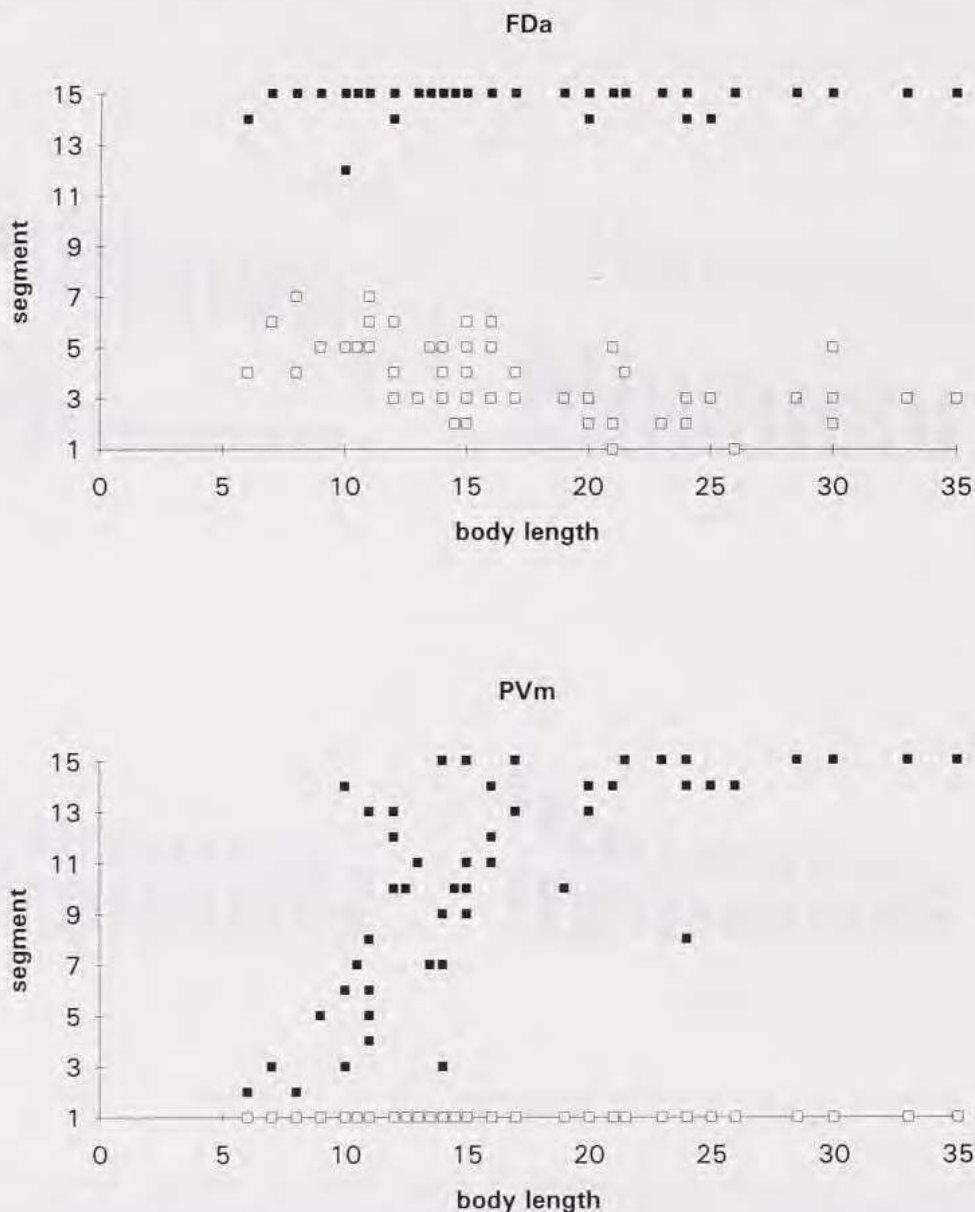


FIG. 4. — Range of segments where the anterior dorsal spine of the femur (FDa, above), and the median ventral spine of the prefemur (PVm, below) occur, in typical representatives of each of the 62 species listed in the Appendix, plotted against average body length (mm). Full squares mark the most anterior segment, empty squares the last segment with the given spine.

Leg size and leg spinulation could be both explained as controlled, over the whole trunk length, by at least two factors acting from centers at both ends of the body.

For those positions where the number of pairs of legs with spines increases with the size of the animal at maturity, two main patterns are observed, one centered in the fore trunk and another centered in the hind trunk (Fig. 4).

#### DISCUSSION

While acknowledging that a definitive evaluation of evolutionary trends, including heterochronies, necessitates a sound and detailed phylogenetic background, such as we cannot yet provide for lithobiids, we believe that our preliminary comparisons of structural and developmental trends are already suggestive of an interesting interplay of strong constraints - such as those keeping together, across a large number of species, body size, number of ocelli, spinulation and number of coxal pores - with the largely independent variation of other traits; at the same time, a great deal of specific differences seem to be easily (we would dare to say: *inexpensively*) obtained by fine-tuning starts, speeds and end points of fundamentally identical processes.

#### APPENDIX-

List of the species whose adult traits were compared (cf. Fig. 2). Data on these species, which are generally listed here under the names used by the authors, were compiled from ANDERSSON (1979), BROLEMANN (1930); EASON (1964), MATIC (1966). Species marked with (L) or (S) are the large or small species considered for the analysis of plectrotaxy as in Figure 3.

- Lithobius (Monotarsobius) aeruginosus* L. Koch, 1862  
*L. agilis pannonicus* Loksa, 1948  
*L. allotyphlus* Silvestri, 1908  
*L. aulacopus* Latzel, 1880,  
*L. (M.) baloghi* Loksa, 1947 (S)  
*L. (M.) biunguiculatus* Loksa, 1947 (S)  
*L. borealis* Meinert, 1872  
*L. bulgaricus* Verhoeff, 1925 (L)  
*L. (M.) burzenlandicus* Verhoeff, 1931 (S)  
*L. calcaratus* C. L. Koch, 1844  
*L. castaneus* Newport, 1844 (L)  
*L. cavernicola* Fanzago, 1877  
*L. (M.) crassipes* L. Koch, 1862  
*L. crypticola* Ribaut, 1926  
*L. (M.) curtipes* C. L. Koch, 1847  
*L. cyrtopus* Latzel, 1880  
*L. (Thracolithobius) dacicus* Matic, 1959  
*L. decapolitus* Matic et al., 1962  
*L. (M.) dobrogicus* Matic, 1962 (S)  
*L. (Dacolithobius) domogledicus* Matic, 1961  
*L. (M.) dubosqui* Brölemann, 1896  
 (= *L. microps* Meinert, 1868) (S)  
*L. (M.) dudichi* Loksa, 1947 (S)  
*L. erythrocephalus* C. Koch, 1847  
*L. fagniezi* Ribaut, 1926  
*L. forficatus* (Linnaeus, 1758) (L)  
*L. inermis* L. Koch, 1856  
*L. (Th.) inexpectatus* Matic, 1962  
*L. lapidicola* Meinert, 1868  
*L. latro* Meinert, 1872  
*L. lucifugus* L. Koch, 1862  
*L. luteus* Loksa, 1947  
*L. matici matici* Prunescu, 1966 (L)  
*L. melanops* Newport, 1845  
*L. (M.) microps* auct. nec Meinert, 1868  
*L. mutabilis* L. Koch, 1862  
*L. muticus* C.L. Koch, 1847  
*L. nicoeensis* (Brölemann, 1904)  
*L. nigrifrons* Latzel, 1880  
*L. nodulipes* Latzel, 1880  
*L. parietum* Verhoeff, 1899 (L)  
*L. pelidnus* Haase, 1888  
*L. peregrinus* Latzel, 1880  
*L. piceus* L. Koch, 1862  
*L. pilicornis* Newport, 1844 (L)  
*L. punctulatus vasconicus* (Chalande, 1905) (L)  
*L. (M.) pustulatus* Matic, 1964  
*L. ribauti* Chalande, 1907  
*L. (M.) sciticus* Prunescu, 1965  
*L. silvivagus* Verhoeff, 1925  
*L. speluncarum* Fanzago, 1877  
*L. (M.) subterraneus* Matic, 1962 (S)  
*L. tricuspis* Meinert, 1872  
*L. troglodytes scutigeropsis* Brölemann, 1930  
*L. typhlus* Latzel, 1886  
*L. variegatus* Leach, 1817  
*Harpolithobius anodus dentatus* Matic, 1957  
*H. banaticus* Matic, 1961 (L)  
*H. intermedius* Matic, 1958  
*H. oltenicus* Negrea, 1962  
*H. radui* Matic, 1955  
*H. triacanthos* Matic, 1964  
*H. tridentatus* Matic, 1962

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